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## Feeding Selectivity and Habitat Usage of *Esox americanus*

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The University of Southern Mississippi

FEEDING SELECTIVITY AND HABITAT USAGE  
OF *ESOX AMERICANUS*

by

Scott Richard Clark

A Thesis  
Submitted to the Graduate School  
of The University of Southern Mississippi  
in Partial Fulfillment of the Requirements  
for the Degree of Master of Science

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August 2011

ABSTRACT

FEEDING SELECTIVITY AND HABITAT USAGE

OF *ESOX AMERICANUS*

by Scott Richard Clark

August 2011

Patterns of piscine prey selection and habitat usage of *Esox americanus* were assessed through a series of field and experimental studies. Although few detailed studies exist on the foraging behavior and habitat usage of *E. americanus*, throughout its range it may be an important trophic component in maintaining fish assemblage structure in many lower order streams. Across 17 sampled streams, the presence of *E. americanus* among reaches within streams was found to be strongly correlated with increasing levels of habitat complexity. Reaches occupied by *E. americanus* featured increased amounts of in-stream physical structure, increased variability in stream width and depth, decreased water temperatures and dissolved oxygen content. Because of its lie-in-wait, ambush attack strategy, habitat complexity was likely a facilitator of prey selection. In a series of outdoor mesocosms experiments featuring alternative forms of structural cover types, four prey species were offered and *E. americanus* exhibited differing intensities of selectivity among prey types. Field selectivity was assessed from 18 sites by clustering species of potential prey assemblages into a series of functional groups using a suite of traits representing species' habitat affinities and morphological characteristics. A pattern of non-random feeding in both field and experimental mesocosm studies indicate that *E. americanus* was selecting prey of a similar body type, choosing soft-rayed, fusiform prey over alternative morphologies.

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CHAPTER I

FEEDING SELECTIVITY AND HABITAT USAGE

OF *ESOX AMERICANUS*

Abstract

Patterns of piscine prey selection and habitat usage of *Esox americanus* were assessed through a series of field and experimental studies. Although few detailed studies exist on the foraging behavior and habitat usage of *E. americanus*, throughout its range it may be an important trophic component in maintaining fish assemblage structure in many lower order streams. Across 17 sampled streams, the presence of *E. americanus* among reaches within streams was found to be strongly correlated with increasing levels of habitat complexity. Reaches occupied by *E. americanus* featured increased amounts of in-stream physical structure, increased variability in stream width and depth, decreased water temperatures and dissolved oxygen content. Because of its lie-in-wait, ambush attack strategy, habitat complexity was likely a facilitator of prey selection. In a series of outdoor mesocosms experiments featuring alternative forms of structural cover types, four prey species were offered and *E. americanus* exhibited differing intensities of selectivity among prey types. Field selectivity was assessed from 18 sites by clustering species of potential prey assemblages into a series of functional groups using a suite of traits representing species' habitat affinities and morphological characteristics. A pattern of non-random feeding in both field and experimental mesocosm studies indicate that *E. americanus* was selecting prey of a similar body type, choosing soft-rayed, fusiform prey over alternative morphologies.



## Introduction

Understanding the underlying factors that facilitate the patterns of the abundance and distribution of organisms has long intrigued ecologists. Morphological features of species provide strong evidence indicating the adaptive evolution to utilize specific space-limited microhabitats (Schlosser and Toth 1984; Matthews 1998) and differential foraging strategies (Keast and Webb 1966; Wainwright and Richard 1995; Wainwright 1996). Connell (1975) and Angermeier and Karr (1983) note that organisms will typically distribute themselves based on three driving ecological factors: the availability of food resources, predation pressure and the physicochemical properties of the environment. Identifying these suites of ecological and environmental conditions is crucial to the understanding of trophic structure and community dynamics.

Habitat complexity is innately associated with the distribution and abundance of aquatic organisms (Poff and Ward 1990). In lotic ecosystems, habitat heterogeneity is strongly influenced by disturbance regimes (Poff and Allan 1995; Matthews 1998), stream morphology (Matthews 1998) and in-stream structural components (Benke et al. 1985; Fausch and Northcote 1992). Physical structure such as rock complexes, in-stream woody debris, aquatic macrophytes and algae allow fishes to gain protection from predators or harsh environmental conditions, to use as foraging microhabitats (Benke et al. 1985; Fausch and Northcote 1992) and spawning sites (Matthews 1998). Compared to homogenous habitats, increasing levels of habitat complexity has been shown to induce strong effects on predator–prey interactions (Savino and Stein 1982; Crowder and Cooper 1982; Werner et al. 1983b; Savino and Stein 1989a; Eklöv and Diehl 1994; Persson and Eklöv 1995; Eklöv 1997; Ostrand et al. 2004; Shoup and Wahl 2009; Carter

et al. 2010), structure community composition (Gorman and Karr 1978; Grossman et al. 1982; Angermeier and Karr 1984; Lobb III and Orth 1991; Matthews 1998) and facilitate differential habitat usage (Werner and Hall 1979; Mittelbach 1981; Werner et al. 1981; Chapman and Mackay 1984; Angermeier and Karr 1984; Eklöv and VanKooten 2001) among stream fishes. Furthermore, habitat complexity will inherently increase the number of available microhabitats, thus expanding total niche space and facilitating a more diverse community. For instance, Angermeier and Karr (1984) showed in reaches enhanced with higher amounts of artificial woody debris, total fish abundance increased and typically contained an enhanced number of large predatory fishes.

Optimal foraging models predict that an animal will theoretically choose prey which maximizes net energy intake, relative to the costs associated with search and handling times (Stephens and Krebs 1986; Galarowicz and Wahl 2005). These components of optimal foraging theory (OFT) are influenced through multiple interactions of suites of traits and behaviors characteristic to predator and prey, such as habitat selection and usage (Werner 1977; Werner et al. 1981; Werner et al. 1983a), environmental variability (Savino and Stein 1982; Shoup and Wahl 2009; Carter et al. 2010), foraging behavior and diet adaptability/flexibility (Gerking 1994), morphology and behavior (Breck 1993), and prey quality (Werner and Hall 1974). Thus, based on the intersection of these characters, species are assumed to forage in a way that the net energy gain of a particular prey item will be greater than the cost of search and handling times associated with consuming that prey item, and are assumed to avoid less profitable prey. Such models have been successful in characterizing predator-prey relations, as well as predicting resource and habitat usage (Mittelbach 1981; Werner et al. 1983a;

Galarowicz and Wahl 2005). Based on these assumptions and tenets of OFT, it is predicted that species foraging behavior will be characterized somewhere along a specialist–generalist gradient. Specialists maximize net energy gain by targeting only high quality prey even if the costs associated with search and handling times are large; whereas generalists attempt to minimize search and handling times by taking any prey available. Thus, variability of resources in the environment will temporally and spatially influence species' relative placement along this continuum.

The choice and rate at which prey are consumed ultimately affect the consumers net energy gain, thereby directly influencing the fitness of predators (Schoener 1971; Osenberg et al. 1988; Mittelbach 1988; Osenberg and Mittelbach 1989). Two driving factors are fundamental in determining the observed patterns of prey usage. Predators are first restricted by the availability of the prey within local community assemblages, and are further limited to those prey items which they can successfully capture and consume; thus the intersection of these two factors will constrain usage of available prey, resulting in the actual diet breadth (Wainwright and Richard 1995). Given this potential range of prey that is available, prey choice will additionally be influenced by three principal factors: the encounter rates of prey, the probability of initiating a feeding strike on an encountered prey item, and the probability of a successful feeding strike (Greene 1983; Osenberg and Mittelbach 1989; Wainwright and Richard 1995). Accordingly, differential rates of consumption among potential prey would be predicted based on both the abundance and distributional patterns of prey, as well as morphological and behavioral characteristics of both the predator (e.g., gape limitation, foraging strategy) and prey (e.g., defense and escape mechanisms, microhabitat selection).

The purpose of this study was to explore patterns of piscine prey selection and habitat usage of *Esox americanus*. By virtue of its fast progression to a piscivorous diet, it is potentially a strong regulator of fish assemblage composition in many small to mid-sized streams where it is often one of a few apex piscivores. Contrasting empirical data exists from field and experimental studies on the degree of selectivity in esocid feeding habits. Previous studies (Beyerle and Williams 1968; Weithman and Anderson 1977; Eklöv and Hamrin 1989; Savino and Stein 1989a) showed that in experimental trials, esocids will typically exhibit a preference towards particular prey items while avoiding others; whereas in field studies, esocids have generally been described as generalist feeders, their diets being primarily influenced by the abundance of available prey (Mann 1982; Raat 1988; Adams 1991; Margenau et al. 1998; Dominguez and Pena 2000), with noted exceptions of exhibited selectivity of certain species (Mauck and Coble 1971; Mann 1982; Eklöv and Hamrin 1989; Alp et al. 2008). Using both a field and experimental component, prey selection on available piscine prey was assessed to determine the generalist nature of prey selection.

Few detailed habitat studies exist in the literature on *E. americanus* and are primarily descriptive in their assessment of habitat usage. Meffe and Sheldon (1988) showed in multivariate space that throughout streams in the upper coastal plains of the Savannah River drainage (South Carolina), *E. americanus* was associated with fish assemblages occupying habitats characterized by abundant detritus and deep, slow-moving, turbid water. Similarly, in Black Creek (Mississippi), Ross et al. (1987) showed that the microhabitats of assemblages containing *E. americanus* typically featured high amounts of in-stream cover, fine substrates, high amounts of detritus and water depths of

over 0.5 m. Cain et al. (2008) found that throughout Indiana streams, *E. americanus* was always associated with either aquatic macrophytes or woody debris and occupied slow-moving habitats. Accordingly, local environmental and physicochemical variables were measured within reaches of 17 sampled streams to assess patterns of habitat usage of *E. americanus*.

## Methods

### *Field Selectivity*

To assess patterns of feeding selection of *E. americanus* on available fishes in the field, *E. americanus* and associated fish assemblages were collected by seining and electro-fishing all available habitat types in 18 small to mid-sized streams throughout the central and southeastern United States (Fig. 1). While both sampling techniques have some inherent bias, a combination of the two ensured a representative estimate of the assemblage structure within each stream. Fish assemblage composition of the immediate and surrounding habitat types allowed for assessment of the possible prey availability for *E. americanus*. Collected fishes were fixed in a 10% formalin solution in the field and later preserved in 70% ethanol for storage and analysis. Fishes were identified to species, enumerated, and all *E. americanus* were measured to the nearest 0.1 mm (standard length, SL). Digestive tracts (esophagus to rectum) were extracted from all *E. americanus* and stomach contents were removed, identified, weighed and enumerated. Upon completion all specimens were cataloged in the University of Southern Mississippi Ichthyological Collection.

Because sampling occurred over a large spatial scale (Fig. 1) and resulted in differential regional species diversity, available prey assemblages were clustered into

functional groups using a suite of functional traits describing species' habitat and morphological characters published by Goldstein and Meador (2004) and Frimpong and Angermeier (2009). Ross (2001) was further consulted to account for local variation in observed traits. Traits included in cluster analysis consisted of species affinities for stream size, microhabitat usage, substrate type, current velocity, in-stream structure usage, presence or absence of spinous fins and type of swimming locomotion. Clustering was performed using *k*-means method, resulting in prey species grouping into four functional groups based on the presence or absence of observed traits. Non-Metric Multidimensional Scaling (NMDS) on Jaccard's dissimilarity metric of the original trait matrix was used to visualize functional grouping established by *k*-means clustering. Starting NMDS configurations were from principal coordinates analysis and convergence on a final configuration was determined from Procrustes analysis (Peres-Neto and Jackson 2001) at each iteration.

The degree of feeding selection for each functional prey group was determined using Chesson's electivity values, assuming prey availability remained constant in sampled assemblages (Chesson 1983). Chesson's electivity values are determined by calculating the selectivity for each functional prey group as

$$\alpha_i = \frac{\left(\frac{r_i}{n_i}\right)}{\sum_{j=1}^m \left(\frac{r_j}{n_j}\right)},$$

where  $n_i$  is the number of individuals within functional prey group  $i$  in sampled assemblages,  $r_i$  is the number of individuals within functional group  $i$  in the diet of the

predator, and  $m$  is the number of available functional groups. These estimated values of  $\alpha_i$  were subsequently centered on zero by the equation

$$\varepsilon_i = \frac{m\alpha_i - 1}{(m - 2)\alpha_i + 1}.$$

Chesson's electivity values can range from  $-1$  to  $+1$ , with a value of  $+1$  indicating complete preference, a value of  $-1$  indicating complete avoidance, and values around zero indicating no preference (i.e., random feeding). A Chi-square test was used to test for patterns of generalist (i.e., random) feeding among the four functional groups. If a generalist pattern of feeding is observed, the proportion of individuals within functional groups in the diet should reflect the proportions in the sampled assemblages. Deviation from this pattern would indicate differential selection by *E. americanus*.

#### *Experimental Prey Selectivity*

Prey selectivity of *E. americanus* was tested using an assemblage of four morphologically distinct species which are often found in association with *E. americanus*. A top-water (*Gambusia affinis*), two pelagic (*Lepomis macrochirus*, *Lythrurus roseipinnis*) and a benthic (*Etheostoma swaini*) species were used as prey in outdoor experimental mesocosms. The prey types further differ in their anti-predatory behavior. Alarm substances are produced by both *G. affinis* and *L. roseipinnis* and are released when an individual is consumed or injured (Ross 2001), thereby alerting conspecifics of a nearby predator. Typical responses to these substances are schooling in tighter aggregations (cyprinids), freezing, and remaining motionless at the water surface (*G. affinis*), or in extreme cases, both may move to the bottom of the streambed and

attempt to remain concealed among the substrate (Ross 2001). In addition to their spinous fins, *L. macrochirus* and *E. swaini* will readily utilize sources of in-stream structure and the substrate to act as refugia from predators.

Predator and prey species were collected by seining and electro-fishing small to mid-sized streams in the Pascagoula River basin (Mississippi, USA). All prey species were collected from environments where predators were present. Prey species were held in separate holding tanks at The University of Southern Mississippi Wet Lab Facility and were fed a diet of frozen food, and *E. americanus* were housed at The University of Southern Mississippi Natural Science Park (USMNSP) and received a diet of live fish. To avoid a conditioning effect of test prey species, *E. americanus* were fed different species (primarily cyprinids) than of those used in trials.

Experimental trials were conducted at USMNSP and each experimental mesocosm ( $N=3$  units used) consisted of a fiberglass tank approximately 0.92 m x 2.44 m x 0.72 m (total volume 1.6 m<sup>3</sup>). Mesocosms were filled with natural gravel and sand substrata to an approximate uniform depth of 4 cm and operational water depth was 65 cm above the substrate. Nylon gill netting (3/8" mesh) was used to cover the top of the enclosures to prevent predator or prey species from escaping mesocosms. Shade was offered in the form of 55% shade cloth above the mesocosms, also ensuring mesocosms did not overheat.

The experimental trials consisted of two treatment groups containing cover types of both live vegetation (*Vallisneria*) and natural woody debris, differing in their relative configuration within the water column. Eighteen stems of *Vallisneria*, arranged in three rows of six across the width of the enclosure provided vegetative cover, and 12 -14 large



pieces of woody debris were piled to serve as an alternative source of cover. One treatment consisted of woody debris occupying the benthic region and vegetation occupied the upper region of the water column. Alternatively, the other treatment was reversed, thus placing the woody debris in the upper region of the water column and the vegetative structure occupied the benthic region. Mesocosms were further divided lengthwise into three sections in which one of each cover types were randomly assigned for placement. Stems of *Vallisneria* were rooted in the substrate when occupying the benthic region of the mesocosm; whereas when in the upper region, stems were rooted in a translucent plastic tub (74 x 48 cm) cut to a depth of 5 cm and filled with similar substrate. A rectangular PVC frame (84 x 53 x 33 cm) with vinyl hardware cloth covering the top side allowed for placement of cover structures in the upper region of the water column.

An assemblage of four randomly selected individuals of each of the four prey species (i.e., 16 total prey items), controlled for size (standard length; SL), were randomly placed into experimental mesocosms and allowed to acclimate for at least 24 h. Any mortality of prey during the acclimation period was immediately replaced and the prey assemblage was further allowed to acclimate until the following day. All trials commenced at 1400 the ensuing day, when a single *E. americanus* (SL range 112 – 188 mm) was introduced into the mesocosm and allowed to feed without restriction. Mortality of prey items discovered during or at the end of a trial period were removed from analyses and electivity calculations were based on adjusted prey proportions. Trials were terminated after five days, tanks were drained and prey remaining was enumerated. Trials in which no prey items were consumed were excluded from analyses. Additional trials (*N*

= 6) without a predator were used as controls to estimate capture efficiency and extrinsic mortality of prey items during the five day trial period.

An alternative derivation of Chesson's electivity values, applicable when multiple prey types are offered and no replacement of consumed items occur throughout the duration of the experiment (Chesson 1983), was used to assess prey selectivity among offered prey. Chesson's electivity values are determined by calculating the selectivity for each prey type as

$$\alpha_i = \frac{\ln\left(\frac{n_{i0} - r_i}{n_{i0}}\right)}{\sum_{j=1}^m \ln\left(\frac{n_{j0} - r_j}{n_{j0}}\right)},$$

where  $n_{i0}$  is the number of prey item  $i$  at the beginning of the experiment,  $r_i$  is the number of prey type  $i$  in the diet of the predator, and  $m$  is the number of available prey types.

Consumption values in trials in which all individuals of one prey type were consumed were adjusted (i.e., value of 3.999) to allow for a defined equation. These estimated values of  $\alpha_i$  were subsequently centered on zero by the equation used in the field analysis.

Electivity values did not conform to normality and were heteroscedastic, therefore a non-parametric analysis of variance (ANOVA) on ranks (Kruskal-Wallis Test) was used to test the overall consumption patterns of the prey species across all trials.

Electivity values were further analyzed using a permutation-based multivariate analysis of variance (PERMANOVA) (Anderson 2001) to test for the effects of the individual enclosures or relative configuration of structure types on consumption patterns among treatments. PERMANOVA is a multivariate analysis of variance which uses permutation

procedures to obtain a probability value. A distribution of pseudo  $F$ -statistics is constructed by permuting the data and is subsequently compared to the original observed  $F$ -statistic to assess a level of significance. Electivity values were analyzed using Euclidean distances, with 100,000 permutations.

### *Habitat Usage*

Seventeen sites were used to assess habitat usage of *E. americanus* throughout the central and southeastern United States (Fig. 1; triangles). At each site, fish were sampled via backpack electro-fishing to specifically target *E. americanus*. When successful captures were made, individual capture locations were marked along the stream bank and were later returned to for data collection. The total sampled reach of each site typically encompassed 150-200 m of the stream length, unless stream characteristics did not allow for efficient sampling of habitats (i.e., drought conditions or depths exceeding electro-fishing ability). Using the marked sampled points, habitats were then delineated into occupied (*E. americanus* present) and unoccupied (*E. americanus* absent) reaches to assess habitat usage. Reach lengths of both occupied and unoccupied habitats were defined as five times the average estimated stream width at three random locations throughout the individually defined reaches. This method effectively standardized available habitat proportional to stream size and allowed for direct comparison within and among sampled stream reaches. An effort was made to separate occupied and unoccupied habitats along the stream reach by a length equivalent to the nearest occupied reach so that associated habitats were not directly adjacent to one another.

Local environmental variables were measured at three points (25, 50 and 75% of stream width) in each defined reach by establishing three transects perpendicular to

stream flow at three positions corresponding to 25, 50 and 75% of reach length. When successful captures of *E. americanus* were made, the middle transect corresponded to the capture location. At each of the nine points, dissolved oxygen (DO), pH, temperature, salinity, conductivity (YSI Professional Plus Series), surface current velocity (Marsh-McBirney Flowmate 2000), depth, dominant substrate based on a modified Wentworth scale (Cummins 1962) and the presence or absence of detritus were measured. At each transect, wetted stream width was recorded and percent canopy cover was estimated (0, 25, 50, 75, 100%). Turbidity (NTU) was measured for the entire reach using a HACH 2100 turbidimeter. The coefficient of variation (CV) of stream depth, stream width, current velocity and dominant substrate were used as measures of habitat heterogeneity. Aquatic vegetation and woody debris were quantified using a 1 m<sup>2</sup> quadrat divided into 100 equivalent grids utilizing the same transects used for local environmental variables. Three quadrats were evenly spaced along each transect; however when stream widths did not permit three replicates per transect (i.e., stream widths < 3 m), additional transects were incorporated directly up- or downstream along the length of the stream within the reach limits. The amount of in-stream physical structure was measured by enumerating grids in which vegetation and/or woody debris was present. Present woody debris was counted in grids which contained woody structure capable of concealing at least 50% of the focal fish's body based on visual estimate of the focal fish's standard length (SL). The CV of physical structure (pooling vegetation and woody debris) was used as a measure of structural patchiness within a defined reach. High CV values would indicate high levels of structural patchiness in a given reach.

To control for the effect of large scale variability between measured habitat and physicochemical variables (i.e., between basins, drainages and streams), data were standardized into  $z$ -scores within sites to allow for direct comparison. Redundancy Analysis (RDA; ter Braak 1994) was used to summarize habitat and physicochemical data from all sampled reaches, by constraining an initial Principal Components Analysis (PCA) by the presence or absence of *E. americanus*. RDA constrains an ordination of response variables of one matrix through a multiple regression approach with predictor variables of a second matrix (Legendre and Legendre 1998). This method is analogous to a Canonical Correspondence Analysis (CCA), where the initial ordination, typically species abundances, is constrained by a matrix of environmental variables (McCune and Grace 2002). An ANOVA permutation test was used to test for a significant effect of the measured environmental variables on the presence/absence of *E. americanus*. Environmental data are permuted and the test statistic of the original data is subsequently compared to the distribution of test statistics of the permuted data to assess a level of significance. All analyses were performed using R statistical software (R Development Core Team 2009).

## Results

### *Field Feeding Selectivity*

A total of 224 *E. americanus* were collected from the 18 sampled sites throughout the central and southeastern United States. Of the 224 stomachs processed, 107 were empty (47.7%) and 117 contained prey items (52.3%) that were dominated by fishes, crustaceans and aquatic insect larvae (94.9% of stomachs containing prey). Non-fish

vertebrates, molluscs and unidentifiable prey comprised the remaining portion of stomach contents.

Across all sampled assemblages, a total of 1809 individuals, representing 47 species were collected co-occurring with *E. americanus*. Clustering successfully grouped assemblage fishes into functional groups based on habitat and morphological characters. Groups were classified based on the functional character with the highest observed frequency within each group and descriptive attributes of each group are summarized in Table 1 (see Appendixes A and B for full trait frequency and species tables). Groups established by functional traits were: Soft-rayed Fins (SORF), Cruiser Locomotion (CL), Backwater Habitat (BWH) and Spiny-rayed Fins (SPRF). The NMDS effectively summarized the functional composition of group inclusion based on *k*-means clustering (Stress = 19.1%; Fig. 2). A pattern of non-random feeding was observed among the four functional groups ( $\chi^2 = 10.21$ , d.f. = 3,  $P < 0.017$ ). Chesson's electivity indicated active selection of two groups, with Chesson's values of 0.33 and 0.20 for the groups SORF and BWH, respectively. Avoidance was observed in the other two groups, Chesson's values indicating moderately strong avoidance of the centrarchid dominated SPRF (Chesson's = -0.60) and the cyprinid dominated CL group (Chesson's = -0.18) (Fig. 3). The SORF group dominated both the proportion of individuals found in both the sampled assemblages (35.1%) and *E. americanus* stomachs (52.4%). The SPRF group was the second most abundant group among assemblage samples (25.2%); however had the lowest observed frequency in stomach contents (7.1%) (Fig. 4).

### *Experimental Feeding Selectivity Trials*

Twenty-two trials were completed using *E. americanus* between 31 July and 10 October 2010. All prey items were successfully recaptured from control trials ( $N = 6$ ), thus it was assumed that fish unaccounted for in predator trials were a direct result of consumption by *E. americanus*. In all trials at least one *G. affinis* was consumed, and on average *E. americanus* consumed 2.45 (range 1 – 4) *G. affinis*, 1.77 (range 0 – 4) *L. roseipinnis*, 0.32 (range 0 – 1) *E. swaini*, 0.23 (range 0 – 1) *L. macrochirus*, and across all trials average consumption was 4.77 (range 1 – 9) individuals during the five day trial period. Two instances of pre-trial mortality resulted in replacement of a single prey item prior to the introduction of *E. americanus*, and similarly in two trials, mortality of a single prey item was recovered during the trial period (prey consumption proportions were subsequently adjusted for these trials). Furthermore, three experimental trials in which no prey were consumed were removed from analyses.

Consumption of prey species by *E. americanus* based on Chesson's electivity values were found to be different ( $H = 55.576$ , d.f. = 3,  $P < 0.001$ ) between the four prey species (Fig. 5). A pairwise post-hoc Tukey comparison indicated median electivity values of both *G. affinis* and *L. roseipinnis* to be significantly different from those of *L. macrochirus* and *E. swaini*; however not significantly different from one another. Similarly, no difference in electivity values was found between *L. macrochirus* and *E. swaini*. PERMANOVA indicated no effect of structural placement or individual mesocosm on consumption patterns of prey species across treatments (Table 2; Fig. 6).

### *Habitat Usage*

Local environmental variables were measured from 62 reaches among the 17 sampled sites, resulting in a total of 25 occupied and 37 unoccupied reaches. The number of unoccupied reaches sampled was typically greater than the number of occupied reaches within a site or if more than one occupied reach was observed, an equal number of unoccupied reaches were sampled; however drought conditions at two sites allowed for only a single paired sampling. In all occupied reaches, *E. americanus* was always found to be located within a reach associated with a source of in-stream structure (mean percentage ranged from 0.01 to 0.36).

Ordination of environmental variables described gradients related to habitat heterogeneity and stream morphology. The first three axes of the RDA together accounted for 39.6% of the total variance among the standardized environmental variables. The constrained proportion of the variability (i.e., presence/absence) was associated completely with RDA axis I and the environmental variables explained one-third (13.2%) of the observed variability in the presence or absence of *E. americanus* (Fig. 7). The first RDA axis accounted for more variation than expected by chance (ANOVA permutation tests,  $N = 1000$  permutations,  $F_{1,60} = 9.139$ ,  $P < 0.001$ ), indicating a significant relationship between the presence/absence of *E. americanus* and environmental variables. Reaches representing occupied and unoccupied habitats separated along RDA axis I and occupied habitats were characterized by increasing amounts of in-stream structure, variability in stream width and depth, lower temperatures and levels of dissolved oxygen.



## Discussion

The presence of *E. americanus* was strongly correlated with increasing levels of habitat heterogeneity (Fig. 6). A stabilizing relationship exists in regards to the effect of increasing levels of habitat complexity on predator-prey interactions. As has been well documented among stream fishes, increasing levels of structural complexity effectively enhances species diversity (Crowder and Cooper 1982; Angermeier and Karr 1984; Matthews 1998), and generally decreases foraging efficiency of piscivorous fishes by inhibiting predator movement, reducing encounter rates with prey and providing refugia for prey (Ostrand et al. 2004; Shoup and Wahl 2009; Carter et al. 2010), therefore intermediate levels of complexity should theoretically maximize predator foraging efficiency (Crowder and Cooper 1979). Foraging success of lie-in-wait piscivores has been shown to increase with intermediate levels of habitat complexity (Savino and Stein 1982; Anderson 1984; Savino and Stein 1989a; Eklöv and Diehl 1994; Eklöv 1997; Ostrand et al. 2004), by cryptically concealing an ambush-style predator to visual detection by potential prey (Coen et al. 1981; Howard and Koehn 1985; Ostrand et al. 2004). For example, Savino and Stein (1989a) found that northern pike (*Esox lucius*) exhibited enhanced foraging success in moderate levels of structural complexity (artificial vegetation) compared to more densely arranged configurations; whereas an active forager, largemouth bass, displayed the opposite pattern (Savino and Stein 1982) and was found to switch to an ambush-style attack at high structure densities (Savino and Stein 1989b).

Woody debris was the dominant structural component in the lowland streams sampled throughout this study. Previous studies investigating the effect of structural

complexity on piscivore feeding have primarily focused on vegetative structure (Anderson 1984; Eklöv and Hamrin 1989; Savino and Stein 1989a; Ostrand et al. 2004), while woody debris as a structural component influencing predator-prey relationships has received little attention. Throughout the mesocosm trials, *E. americanus* did not indicate a preference for either woody debris or *Vallisneria* when choosing available prey. Similar patterns of foraging were observed independent of structural configuration (Fig. 6), indicating that predatory selection appears to be determined by the species of prey rather than being influenced by available structure types. Based on the observed foraging behavior, the upper portion of the water column provided the most profitable foraging grounds. This was most likely a function of the relative visual detectability of *G. affinis* and *L. roseipinnis*. The top-water *G. affinis* was typically observed throughout trials occupying the outer margins of the structural component present in the upper portion of the water column or along the sides of the mesocosms. *Lythrurus roseipinnis* was routinely observed schooling in the “open” portions of the mesocosms (i.e., no structural components), and as similarly noted by Ross (2001), were generally occupying the upper portion of the water column. These behaviors may have provided *E. americanus* with enhanced detection ability and encounter rates with these species, contributing to their selection relative to the other prey. The presence of structure possibly decreased encounter rates of both *L. macrochirus* and *E. swaini*, based on their anti-predatory and cryptic behaviors. Neither species was readily observable during trials, *E. swaini* remaining cryptically concealed among the sand and gravel substrate, whereas *L. macrochirus*, when observed, was typically found in association with an available cover type.

Experimental studies with esocids (Beyerle and Williams 1968; Mauck and Coble 1971; Weithman and Anderson 1977; Moody et al. 1983; Wahl and Stein 1988; Eklöv and Hamrin 1989; Savino and Stein 1989a), largemouth bass (Savino and Stein 1989a) and spotted gar (Ostrand et al. 2004) have shown that when given a choice of prey, soft-rayed fishes are strongly preferred over their spiny-rayed counterparts. In this study, both mesocosm and field data show that *E. americanus* displayed differential feeding selection among prey species and functional groups, respectively. Prey selection was dominantly directed towards soft-rayed fishes, with the majority of the consumed prey adapted for inhabiting and foraging along the water surface (i.e., *Fundulus spp.*, *G. affinis*). These surface-oriented fishes may be prone to an increased threat of predation, becoming more perceptible to lie-in-wait, visual predators (Eklöv and Hamrin 1989). As habitat complexity increases, certain prey types may be encountered less frequently in highly structured environments (Savino and Stein 1982; Anderson 1984; Savino and Stein 1989a; Shoup and Wahl 2009; Carter et al. 2010), thus the relative ability of predators to detect conspicuous surface-oriented fishes may be further enhanced. Therefore the success of an ambush predator may be determined not only by levels of increasing habitat complexity, but also the type and behavior of potential prey. Prey availability was likely an important facilitator of habitat usage of *E. americanus* that was not accounted for in this study, thus further research is needed to address how the abundance and distributional patterns of prey species affect the habitat usage of *E. americanus* across spatial and temporal scales. Chapman and Mackay (1984) showed that large northern pike in an Alberta lake were extremely versatile in their habitat usage in both space and time, and suggested such behavior is advantageous to exploit prey resources in all

available habitat types. Smaller size classes were restricted to the vegetated littoral zones, mainly being attributed to predator avoidance; whereas larger pike were released from such predation pressures and utilized a broader range of habitats. Similarly, in the small- to mid-sized streams sampled throughout this study, small *E. americanus* (<100 mm) may be limited in their foraging ability among available habitat types, while larger adults may have the ability to utilize all available habitat types, and thus a larger portion of the prey present.

Centrarchid species dominated (>25% total relative abundance) half of the sampled field assemblages; however only a single individual was present among stomach contents. Morphological and behavioral features of centrarchids may explain their strong avoidance in the diet in both mesocosm and field studies. First, gape limitation of *E. americanus* may inhibit successful capture, manipulation and ingestion of the relatively deeper-bodied centrarchids. Secondly, attacks by esocids are often directed at the midbody of prey (Webb and Skadsen 1980), thus the presence of spines may further constrain the ability to consume centrarchid prey and may increase the risk of predator mortality. Moody et al. (1983) noted that attacks by tiger muskellunge (*Esox lucius* x *E. masquinongy*) on bluegill were redirected towards the caudal region, decreasing the rate of successful captures. Third, many centrarchid species have been shown to have a high affinity for structure (Werner 1977; Mittelbach 1981; Werner et al. 1983b; Savino and Stein 1989a) and that, combined with their high degree of maneuverability (Keast and Webb 1966; Moody et al. 1983), provide an effective escape mechanism from predatory attacks. Consequently, from an optimization standpoint, the relative cost associated with search and handling times may reduce the profitability of centrarchid prey, facilitating the

use of other prey types by predators. Northern pike that occurred in lakes dominated by small edible bluegill were found to feed primarily on aquatic insects, crayfish and tadpoles, avoiding the abundant spiny-rayed centrarchids (Beyerle 1978). In addition, Wahl and Stein (1988) found that in both laboratory and field studies, that three esocids (*E. lucius*, *E. masquinongy* and *E. lucius* x *E. masquinongy*) consumed fewer prey and exhibited decreased growth rates when bluegills (*Lepomis macrochirus*) were the only prey item present than when gizzard shad (*Dorosoma cepedianum*) was offered as an alternative prey. They further showed that the relative handling times were higher for bluegill compared to gizzard shad and fathead minnows (*Pimephales vigilax*).

The avoidance of the CL group was likely attributed to the microhabitat selection of species comprising this group. This functional group dominantly featured cyprinid species that often exhibit a tendency to occupy areas of swifter moving current velocities and larger stream sections. *Esox americanus* tends to avoid such microhabitats (Meffe and Sheldon 1988; Cain et al. 2008), and depending on geographic location, is often replaced by larger congeners *E. niger* in the south and east and *E. lucius* in the upper Mississippi River and Great Lakes regions when current velocities and stream sizes increase (Crossman 1966). Thus the combination of the CL group containing the fewest number of individuals (Table 1; Fig. 4) from the sampled assemblages and therefore relatively low rates of encounter rates compared to the other functional groups, resulted in a minimal contribution to the diet of *E. americanus*.

Throughout mesocosm and field studies, *E. americanus* appeared to exhibit an optimal feeding strategy given the available prey. Prey selection predominately focused on fusiform-bodied prey with absent or minimal morphological defenses. The selection of

prey by northern pike has been suggested to be affected by prey morphology, with pike preferring soft-rayed, fusiform prey (Mauck and Coble 1971; Eklöv and Hamrin 1989; Alp et al. 2008) indicating selective behaviors targeting particular body types. Esocids have been described as keystone predators and are assumed to regulate piscine prey assemblages through their early ontogenetic switch to piscivory and high reliance on fish as a dominant staple of the diet as adults (Keast 1985; Casselman and Lewis 1996; Mittelbach and Persson 1998). The results from this study indicate that *E. americanus* could potentially regulate the abundance of prey species of select body morphologies across its range.

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TABLE 1. Classification of functional groups based on *k*-means clustering of species habitat affinities and morphological characters of sampled assemblages. Groupings were named based on the functional character with the highest observed frequency within each group. The defining functional characters with observed frequencies, abundant species, number of species, individuals and individuals consumed within each functional group are listed. See Appendixes I and II for full character frequency and species group inclusion tables.

Group	Functional Traits (% Observed)	Representative Species	# of Species	# of Individuals	# Consumed
Soft-rayed Fins (SRF)	Soft-rayed Fins (0.89) Backwater Habitat (0.78) Accelerator Locomotion (0.78)	<i>Gambusia affinis</i> <i>Fundulus olivaceus</i> <i>Labidesthes sicculus</i>	9	634	22
Cruiser Locomotion (CL)	Cruiser Locomotion (0.70) Run Habitat (0.70) Moderate Current Velocity (0.70) Large River Habitat (0.60)	<i>Lythrurus roseipinnis</i> <i>Notropis texanus</i> <i>Cyprinella whipplei</i>	10	305	5
Backwater Habitat (BWH)	Backwater Habitat (1.00) Detritus Present (0.93) Large Woody Debris (0.87)	<i>Esox americanus</i> <i>Lythrurus fumeus</i> <i>Notemigonus crysoleucas</i>	15	415	12
Spiny-rayed Fins (SPRF)	Spiny-rayed Fins (0.85) Detritus Present (0.62) Creeper Locomotion (0.54)	<i>Lepomis macrochirus</i> <i>Lepomis megalotis</i> <i>Erinnyzon tenuis</i>	13	455	3



TABLE 2. PERMANOVA results of Chesson's electivity values of prey selection using Euclidean distances in mesocosm trials by *E. americanus*. Treatments reflect randomized configuration of structural components with each trial.

Source	d.f.	SS	MS	<i>F</i> -statistic	$r^2$	<i>P</i> -value
Treatment	1	0.2320	0.2320	0.6731	0.0322	0.5228
Mesocosm	2	0.7758	0.3879	1.1256	0.1076	0.3560
Residuals	18	6.2031	0.3446		0.8602	
Total	21	7.2109			1.0000	

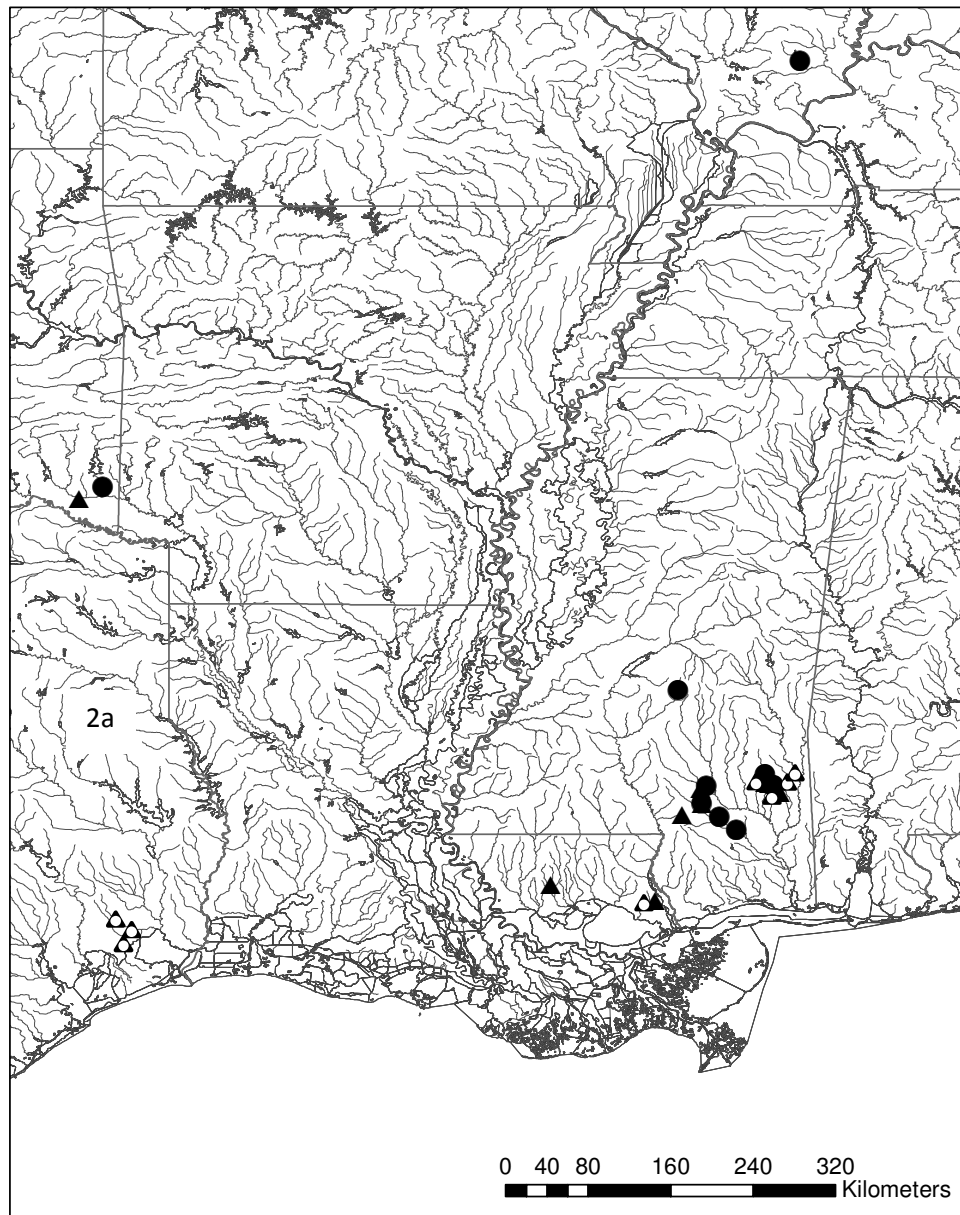


FIG. 1. Sampling sites for diet selectivity and habitat analyses of *E. americanus* throughout the central and southeastern United States. Circles and triangles represent sites exclusively sampled for selectivity and habitat analyses, respectively. Triangles interlaid with a circle represent sites in which data for both selectivity and habitat analyses were collected.

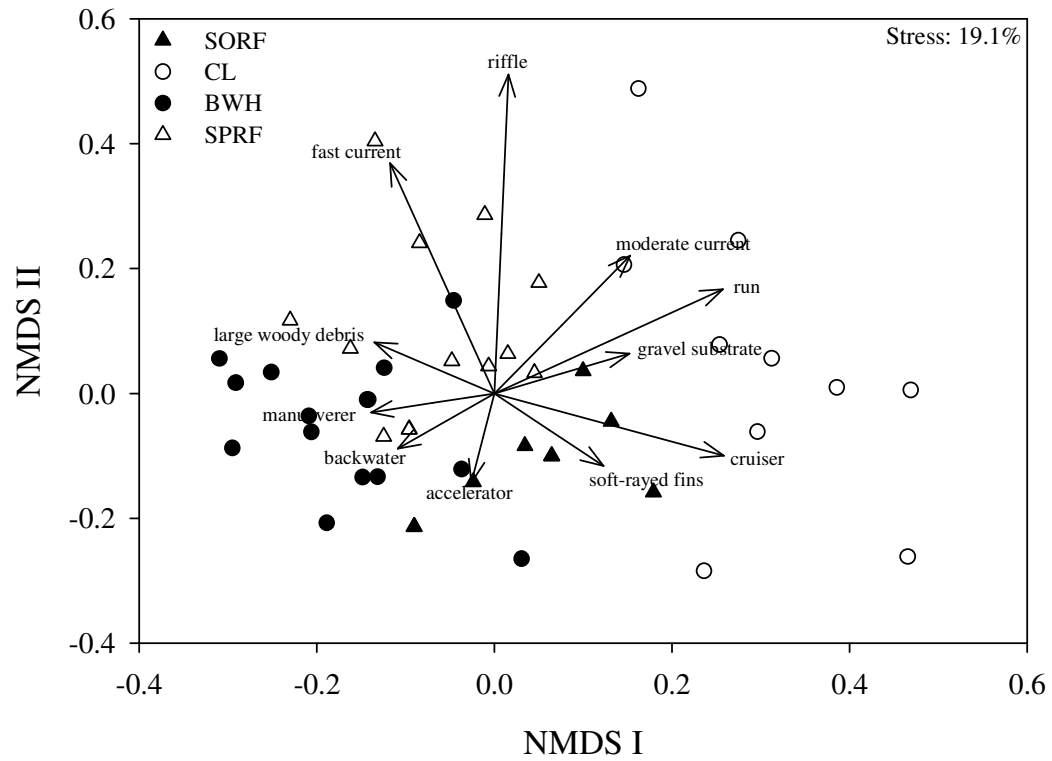


FIG. 2. Ordination of species group inclusion using non-metric multidimensional scaling (NMDS). Shapes and shading indicate group inclusion based on *k*-means method of divisive clustering.

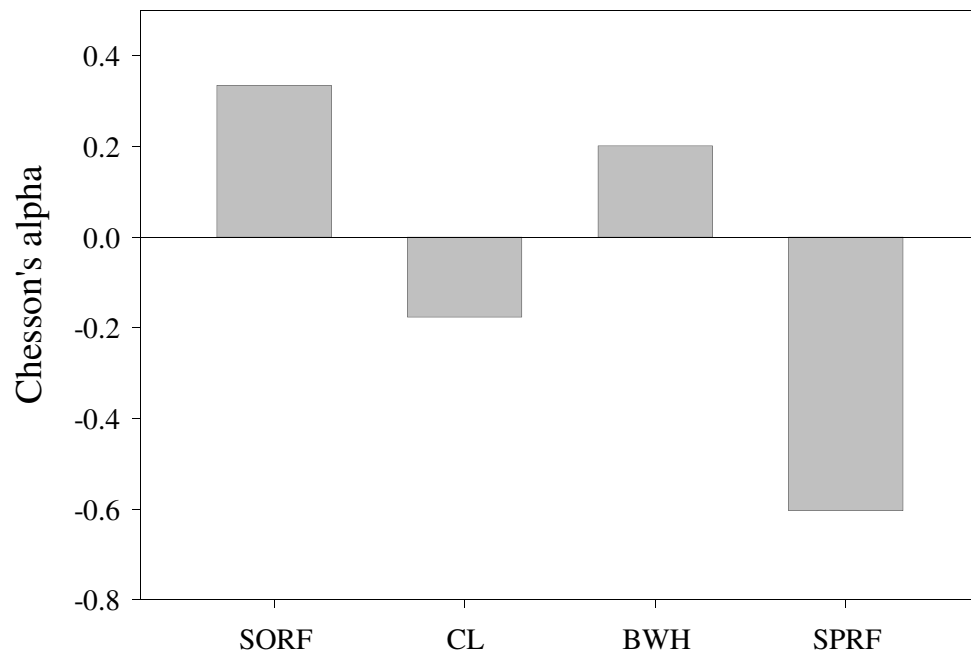


FIG. 3. Centered Chesson's electivity values of *E. americanus* consumption on the four prey assemblage functional groups clustered using *k*-means method. Positive electivity values indicate active selection, negative values indicate avoidance and values near zero indicate random selection of prey.

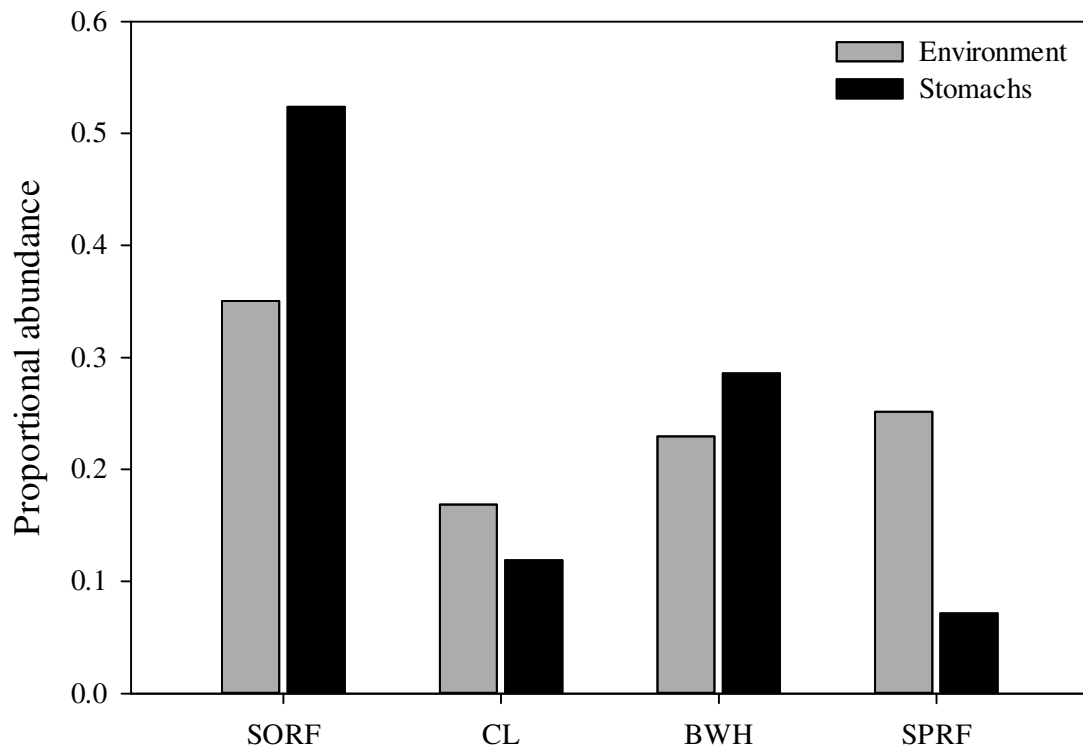


FIG. 4. Proportional abundance of four prey assemblage functional groups found in environment and stomachs of *E. americanus*. A non-random pattern of feeding was observed among the four functional groups ( $\chi^2 = 10.21$ , d.f. = 3,  $P < 0.017$ ).

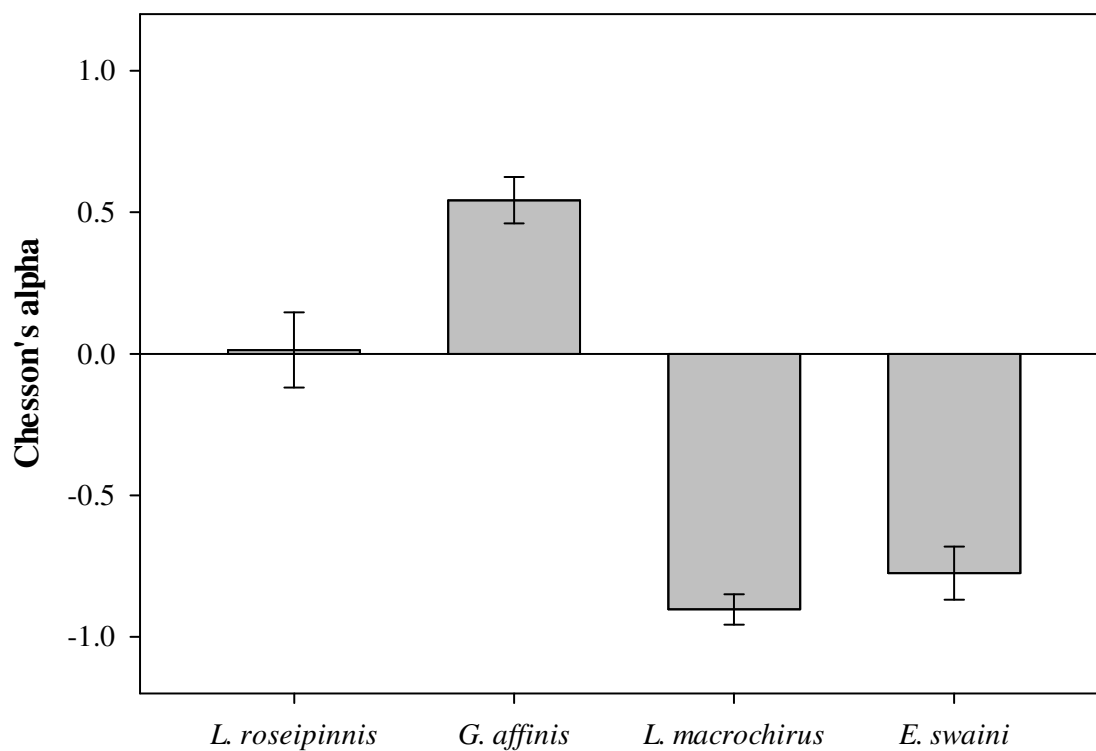


FIG. 5. Centered Chesson's electivity values ( $\pm 1$  SE) of *E. americanus* consumption on the four test prey species. Initial prey availability was four individuals from each of the four species.

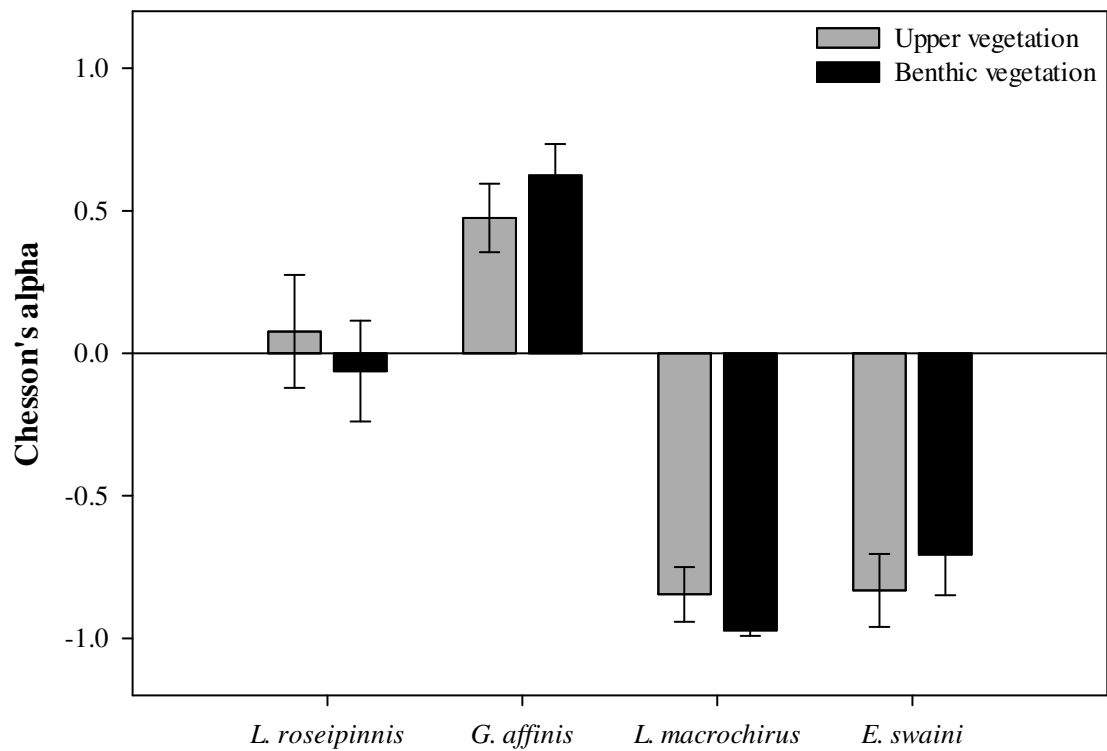


FIG. 6. Centered Chesson's electivity values ( $\pm 1$  SE) of *E. americanus* consumption on the four test prey species between treatments of structural placement. Treatments consisted of random configurations of structural components occupying the benthic and water column regions of mesocosms.

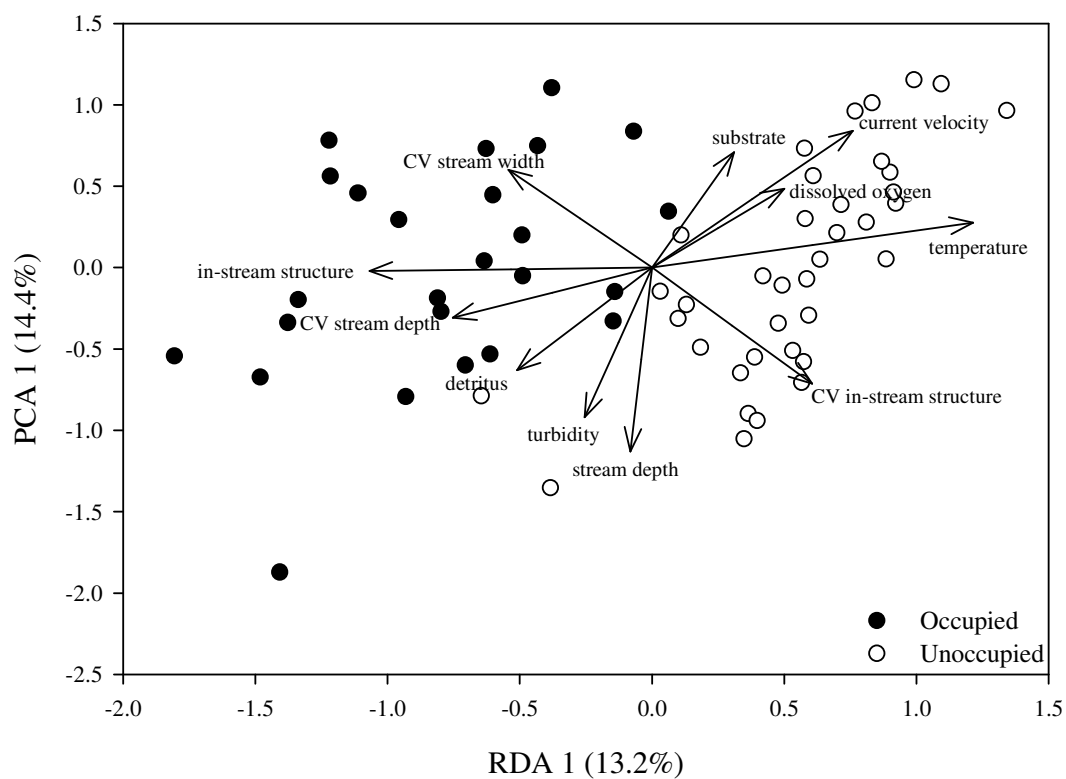


FIG. 7. Redundancy analysis (RDA) of all standardized physicochemical and habitat variables measured within sampling reaches. Individual reaches represented by individual points and shaded by occupancy.



## APPENDIX A

OBSERVED FREQUENCY OF FUNCTIONAL TRAITS AMONG THE FOUR  
FUNCTIONAL ASSEMBLAGE GROUPS

Trait category	Functional Trait	Functional Group (% Frequency)			
		SORF	CL	BWH	SPRF
Stream Size	Creek	1.00	0.80	0.93	1.00
	Small River	1.00	1.00	0.93	1.00
	Large River	0.22	0.60	0.67	0.31
Current Velocity	Slow	1.00	0.80	1.00	0.85
	Moderate	0.00	0.70	0.00	0.31
	Fast	0.00	0.00	0.00	0.15
Microhabitat	Riffle	0.00	0.10	0.00	0.08
	Run	0.00	0.70	0.00	0.15
	Pool	1.00	0.80	1.00	0.85
	Backwater	0.78	0.10	1.00	0.38
	Variable	0.00	0.00	0.00	0.08
Substrate	Muck	1.00	0.10	0.73	0.92
	Silt	1.00	0.10	0.67	1.00
	Sand	0.78	0.80	0.40	0.92
	Gravel	0.67	0.90	0.07	0.46
	Cobble	0.44	0.40	0.07	0.00
	Boulder	0.22	0.00	0.07	0.00
	Bedrock	0.22	0.00	0.07	0.00
In-stream Structure	Detritus	0.11	0.20	0.93	0.62
	Vegetation	0.89	0.50	0.93	0.85
	Large Woody Debris	0.00	0.20	0.87	0.23
Locomotion	Cruiser	0.22	0.70	0.13	0.00
	Accelerator	0.78	0.00	0.13	0.00
	Creeper	0.00	0.20	0.33	0.54
	Manueverer	0.00	0.00	0.40	0.46
	Specialist	0.00	0.10	0.00	0.00
Fin Morphology	Spiny-rayed Fins	0.11	0.30	0.73	0.85

## APPENDIX B

LIST OF SPECIES, OCCURRENCE, ABSOLUTE AND PROPORTIONAL  
ABUNDANCES OF SPECIES COMPRISING FUNCTIONAL GROUPS

Functional Group	Species	Total Occurrences	Total Abundance	Percent Abundance
Soft-Rayed Fins (SORF)	<i>Gambusia affinis</i>	12	361	19.96
	<i>Fundulus olivaceus</i>	11	87	4.81
	<i>Labidesthes sicculus</i>	4	63	3.48
	<i>Luxilus chrysocephalus</i>	2	56	3.10
	<i>Fundulus notti</i>	2	25	1.38
	<i>Fundulus chrysotus</i>	2	18	1.00
	<i>Pteronotropis signipinnis</i>	2	14	0.77
	<i>Fundulus notatus</i>	3	6	0.33
	<i>Fundulus blairae</i>	2	4	0.22
Spiny-rayed Fins (SPRF)	<i>Lepomis macrochirus</i>	15	148	8.18
	<i>Lepomis megalotis</i>	12	109	6.03
	<i>Erimyzon tenuis</i>	3	88	4.86
	<i>Erimyzon oblongus</i>	7	43	2.38
	<i>Lepomis miniatus</i>	10	34	1.88
	<i>Percina nigrofasciata</i>	3	15	0.83
	<i>Etheostoma swaini</i>	4	8	0.44
	<i>Etheostoma chlorosoma</i>	1	3	0.17
	<i>Etheostoma gracile</i>	1	3	0.17
	<i>Ambloplites ariommus</i>	1	1	0.06
	<i>Lepomis marginatus</i>	1	1	0.06
	<i>Lepomis microlophus</i>	1	1	0.06
	<i>Noturus nocturnus</i>	1	1	0.06
Cruiser Locomotion (CL)	<i>Lythrurus roseipinnis</i>	3	124	6.85
	<i>Notropis texanus</i>	5	67	3.70
	<i>Cyprinella whipplei</i>	1	48	2.65
	<i>Micropterus punctulatus</i>	9	29	1.60
	<i>Opsopoeodus emiliae</i>	1	13	0.72
	<i>Cyprinella venusta</i>	2	10	0.55
	<i>Etheostoma stigmaeum</i>	2	9	0.50
	<i>Ichthyomyzon gagei</i>	2	2	0.11
	<i>Noturus leptacanthus</i>	1	2	0.11
	<i>Dorosoma cepedianum</i>	1	1	0.06

Functional Group	Species	Total Occurrences	Total Abundance	Percent Abundance
Backwater Habitat (BWH)	<i>Esox americanus</i>	12	208	11.50
	<i>Lythrurus fumeus</i>	2	63	3.48
	<i>Notemigonus crysoleucas</i>	3	32	1.77
	<i>Aphredoderus sayanus</i>	12	31	1.71
	<i>Lepomis gulosus</i>	10	27	1.49
	<i>Etheostoma proeliare</i>	2	20	1.11
	<i>Pomoxis annularis</i>	2	12	0.66
	<i>Ameiurus natalis</i>	4	7	0.39
	<i>Elassoma zonatum</i>	3	5	0.28
	<i>Lepomis cyanellus</i>	3	3	0.17
	<i>Esox niger</i>	2	2	0.11
	<i>Pomoxis nigromaculatus</i>	1	2	0.11
	<i>Ameiurus melas</i>	1	1	0.06
	<i>Centrarchus macropterus</i>	1	1	0.06
	<i>Noturus gyrinus</i>	1	1	0.06

## APPENDIX C

## INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE APPROVAL FORM



The University of  
Southern Mississippi

*Institutional Animal Care  
and Use Committee*

118 College Drive #5147  
Hattiesburg, MS 39406-0001  
Tel: 601.266.6820  
Fax: 601.266.5509  
[www.usm.edu/spa/policies/animals](http://www.usm.edu/spa/policies/animals)

**INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE  
NOTICE OF COMMITTEE ACTION**

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER: **09051404**  
PROJECT TITLE: **Trophic Ecology and Habitat Partitioning in Southern Populations of the Chain Pickerel, *Esox niger***  
PROPOSED PROJECT DATES: **05/01/2009 to 11/20/2010**  
PROJECT TYPE: **New Project**  
PRINCIPAL INVESTIGATOR(S): **Jake Schaefer, Ph.D.**  
COLLEGE/DIVISION: **College of Science & Technology**  
DEPARTMENT: **Biological Sciences**  
FUNDING AGENCY/SPONSOR: **Departmental**  
IACUC COMMITTEE ACTION: **Full Committee Review Approval**  
PROTOCOL EXPIRATION DATE: **09/30/2011**

  
Robert C. Bateman, Jr., Ph.D.  
IACUC Chair

5-14-09  
Date